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DYNAMICS OF THE STRIKE IN *AGRION* (SYN. *CALOPTERYX*) *SPLENDENS* HARRIS 1782 LARVAE (ODONATA: *CALOPTERYGIDAE*)

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In *Agrion splendens* larvae, the sequence of capture has been studied in detail. During the strike, a very quick forward and backward movement of the foregut can be seen which is synchronous respectively with extension and retraction of the mask. A hydraulic mechanism for the projection of the mask is considered, assuming that the absence of thoracic and abdominal diaphragmatic muscles is compensated by the narrowness of the abdomen.

INTRODUCTION

The projection of the mask, in *Agrion splendens* larvae, can be elicited by stimulating antennae or tarsi with preys or models (CAILLÈRE, 1965, 1968). In anisopteran larvae, PRITCHARD (1965) has shown in *Aeshna* that the projection of the mask is synchronous with the dorso-ventral contraction of the abdomen and with the closing of the anal processes. Later, RICHARD (1970) studied the details of the strike and found in particular that, before the mask is projected toward the prey, the labial base is loosened.

In old *Agrion splendens* larvae observed from above under the binocular microscope, one can see very rarely, during the capture, a very quick forward and backward movement of the oesophagus, like a piston movement. To my knowledge, this has not been previously reported. It seemed interesting, therefore, to study this in detail. This paper deals with the analysis of the phenomena which occur before, during, and after the strike.

METHODS

In old larvae, the integument is not transparent enough to observe the precise details of the movements in the digestive tract. Thus the capture of prey has been studied in young larvae, where the transparency of the integument enables the phenomena which occur to be followed.

Fourth instar larvae (about 5 mm in length) were filmed with a ciné camera, at a speed of 64 frames per second and drawings made from the negatives. Hence, six parameters were investigated: the variations of the angle between the two palps, the displacement of the mentum, the displacement of the digestive tract, the variations in length of the abdomen, the variations of the angle between the lateral caudal gills, and the variations of the angle between the two scapes. To follow the displacement of the digestive tract, the larvae were fed with one prey a day before the films were taken. Consequently, the digestive tract was seen dark, and its outlines could be drawn.

RESULTS

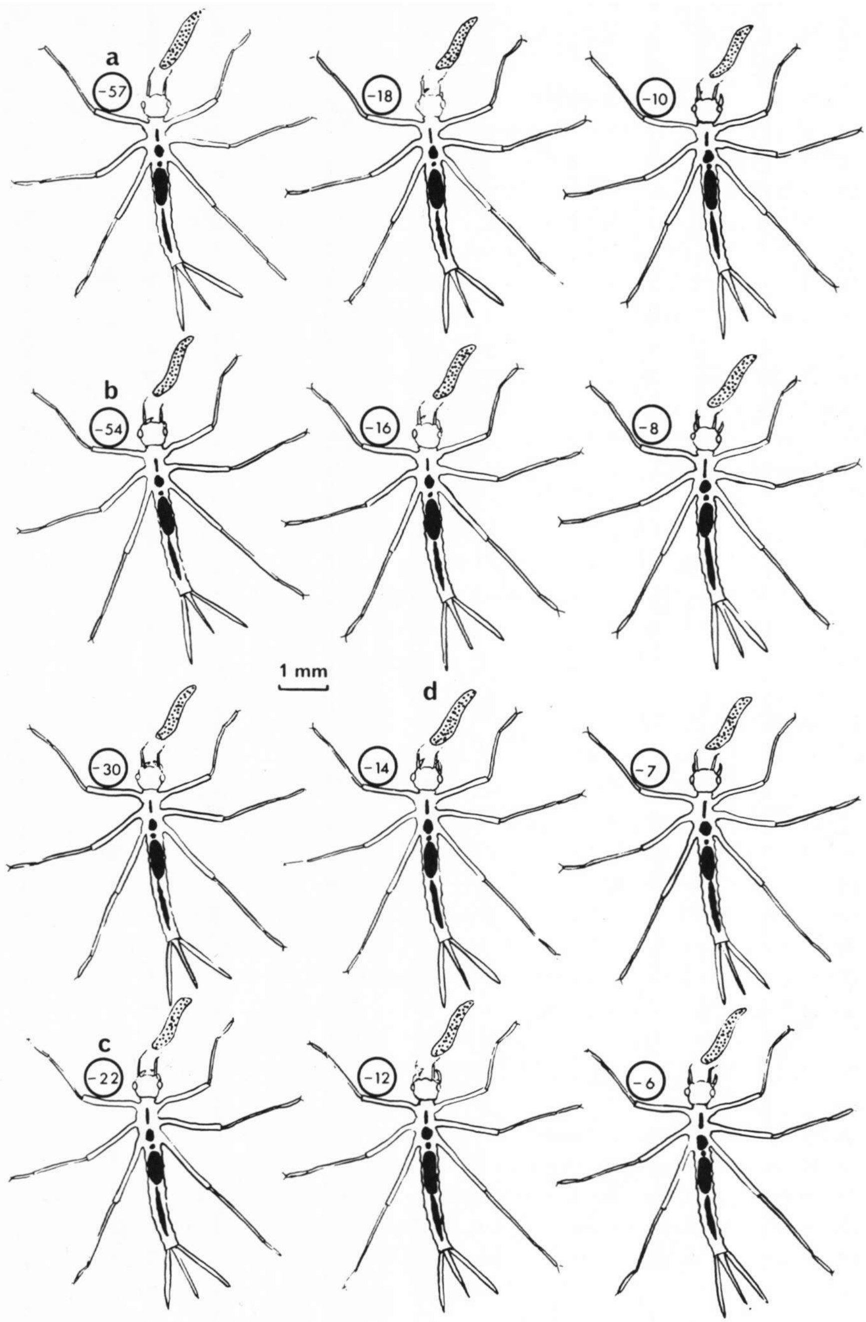
One can distinguish three phases: the preliminaries of the capture, the extension, and the retraction of the mask. For these, the reader should examine Figures 1-4.

I. Preliminaries of the capture

For these preliminaries which occur at the end of the sequence of exploration (Fig. 1), first the lateral caudal gills begin to converge (a), then the head is slightly raised up, because the palps can be seen (b). The convergent movement of the gills continues while the palps begin to open (c). With the acceleration of the convergence of gills, the digestive tract moves very slightly forward (d), as also does the mentum, and the antennae begin to lift. Then the piston movement of the digestive tract and the shortening in length of the abdomen begin, the antennae continuing to rise (Fig. 2e).

II. Extension of the mask

Finally the post-mentum is loosened (Figs. 2f, 5). Suddenly, the mask is projected towards the prey (Figs. 2g, 6) and continues its forward movement (g). The palps, completely open in (g), grasp the prey (h). The mask is fully extended (Figs. 7 – 8) when the digestive tract has stopped its forward movement, and at the same time the convergent movement of the gills ceases (Fig. 2i).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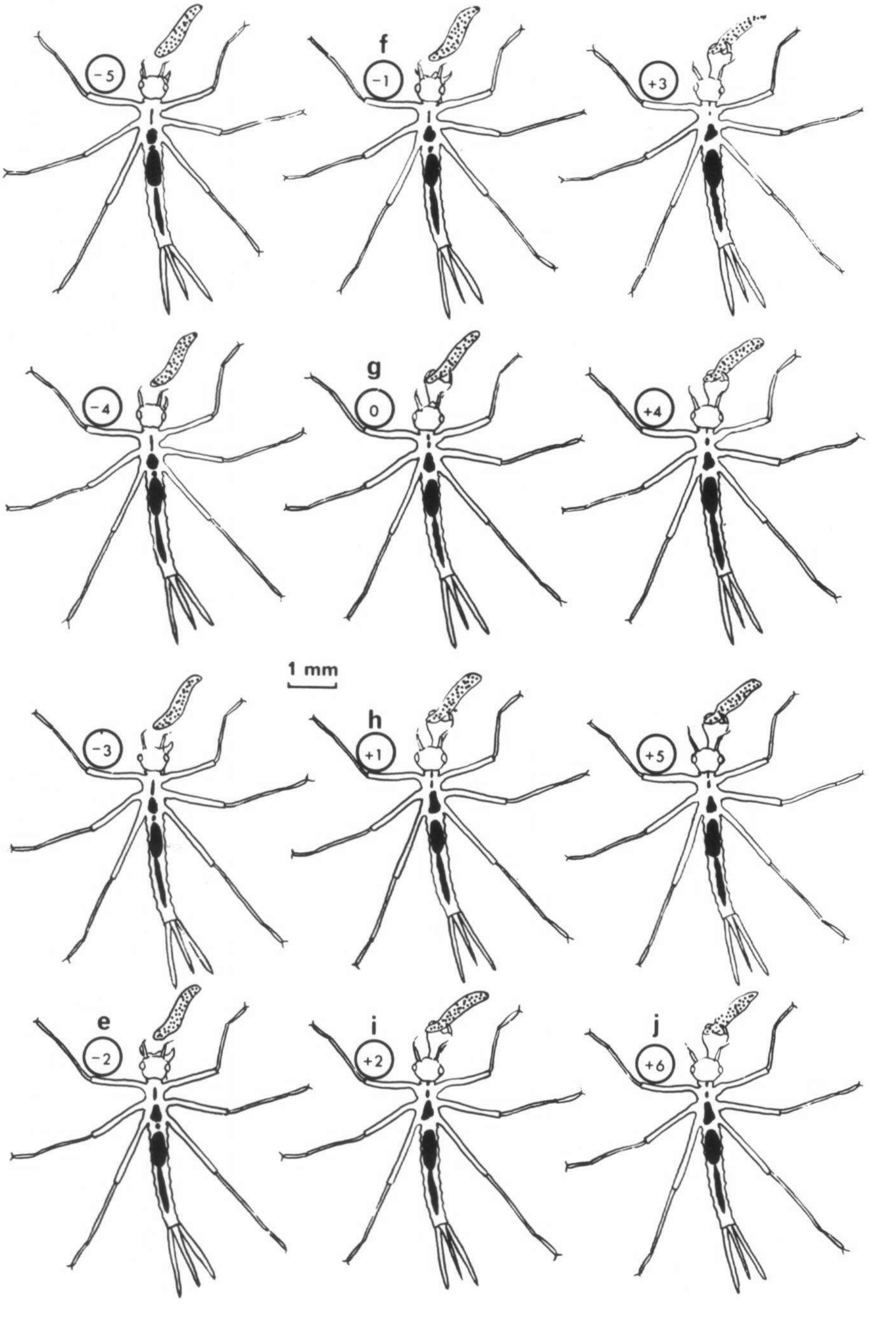
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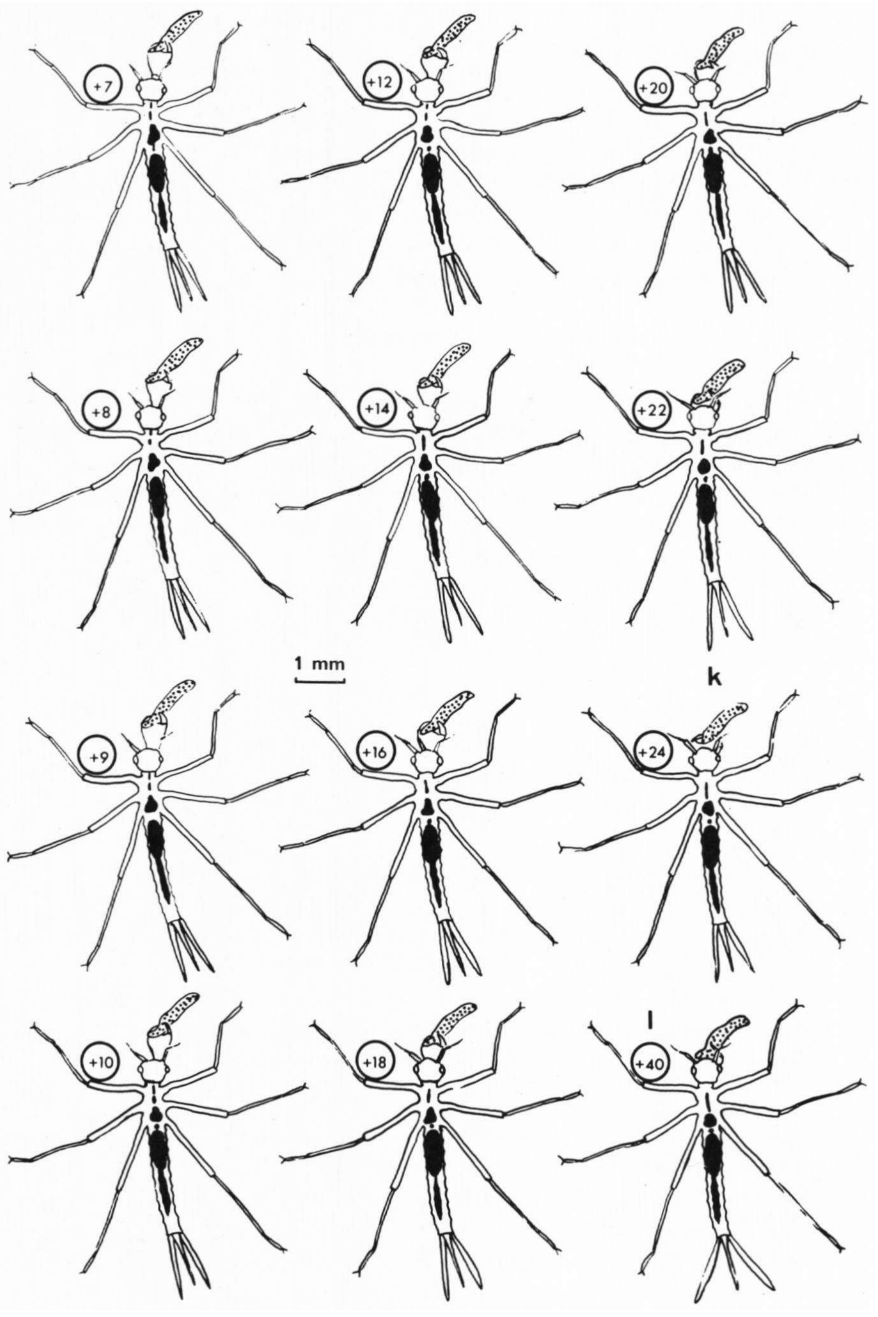


Figs. 1-3. Drawings of 4th instar larvae from ciné film, taken at a speed of 64 fr./sec. The outlines of the digestive tract are blackened. Negative numbers indicate the number of frames before the mask is projected, positive numbers the number of frames after it is projected. (a, b, c, ... , l, cf. text).

III. Retraction of the mask

The prey being firmly grasped (Fig. 2j), the mask, the digestive tract and the abdomen return to their original position, and the lateral caudal gills begin to diverge. Note that the retraction of the mask is synchronous with the return of the digestive tract (Fig. 3k). The stability in the angle between the scapes indicates that ingestion occurs (Fig. 3l), the caudal gills being returned to their original position. During ingestion, the gills are often more divergent.

DISCUSSION

The duration of the sequence of capture in 4th instar larvae is quite different from that in last instar larvae (cf. Table I). The opening of the palps, slow in the 4th instar, is very fast in the last instar. In the 4th instar the mask is fully extended in 35 msec, i.e. 2.5 times slower than in the last instar (15 msec). The retraction of the mask occurs in 0.34 sec in the 4th instar, i.e. is from 3 to 4 times slower than in the last instar (0.080-0.11 sec.).

Table I

Species and instar		Duration in seconds			
		1	2	3	4
Agrion splendens	4th instar	0.38	0.015	0.035	0.340
	last (12th) instar	0.015	0.015	0.015	0.080-0.11
Aeshna or *Anax* (RICHARD, 1970)		0.050	0.010	0.010	0.125

(1) opening of the palps; – (2) loosening of the mask; – (3) extension of the mask; – (4) retraction of the mask.

The comparison of our results with the observations of RICHARD (1970) in *Aeshna* and *Anax* larvae indicates that the time spent for the forward and backward motion of the mask is practically the same in last instar *Agrion splendens* larvae (0.125 sec) and in *Aeshna* or *Anax* (0.135 sec). However, for the duration of the opening of the palps, *Aeshna* and *Anax* larvae fixate on the prey for about 3 times longer than *Agrion splendens*. This difference is probably due to fundamental differences in the behaviour of these animals: in Aeshnidae, the fixation is mainly effected by means of visual stimuli, whereas in *Agrion splendens* larvae,

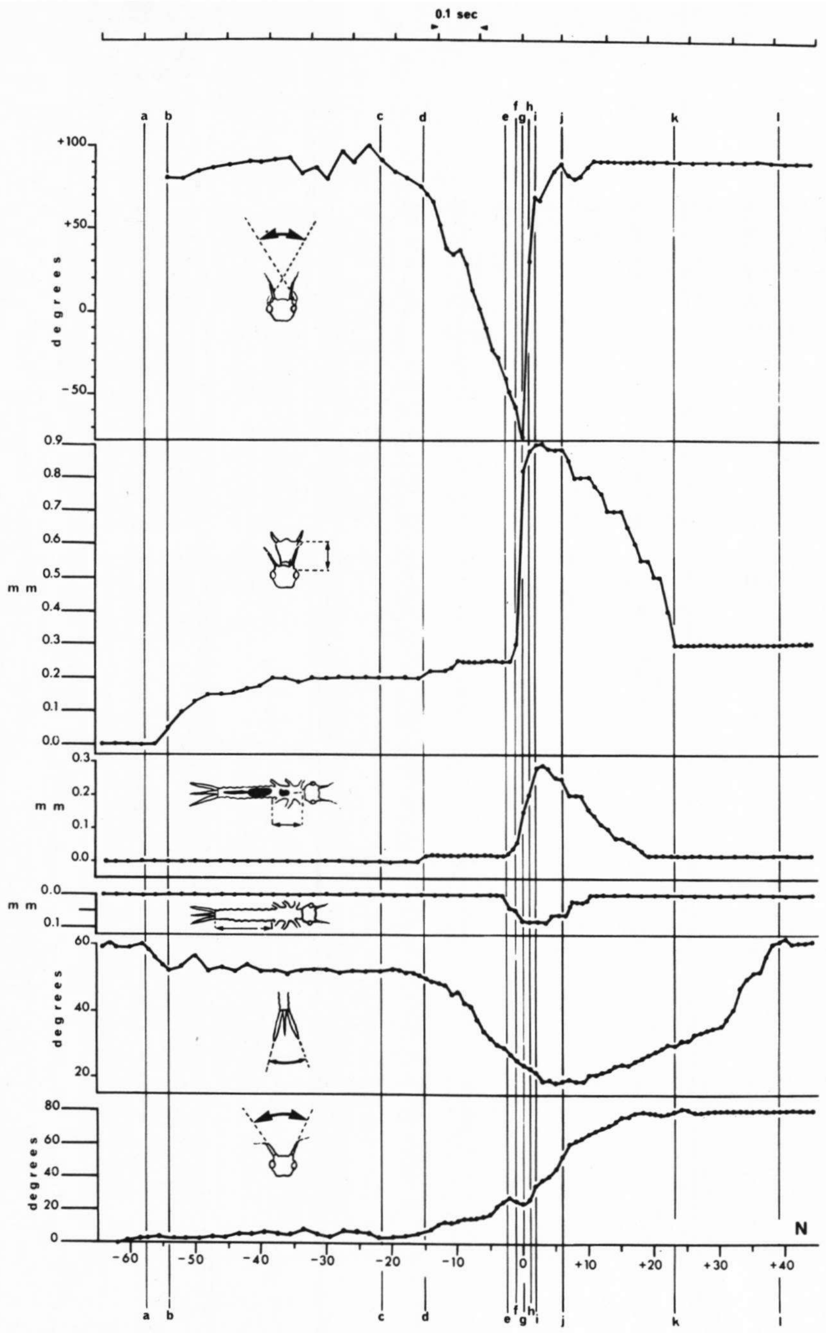
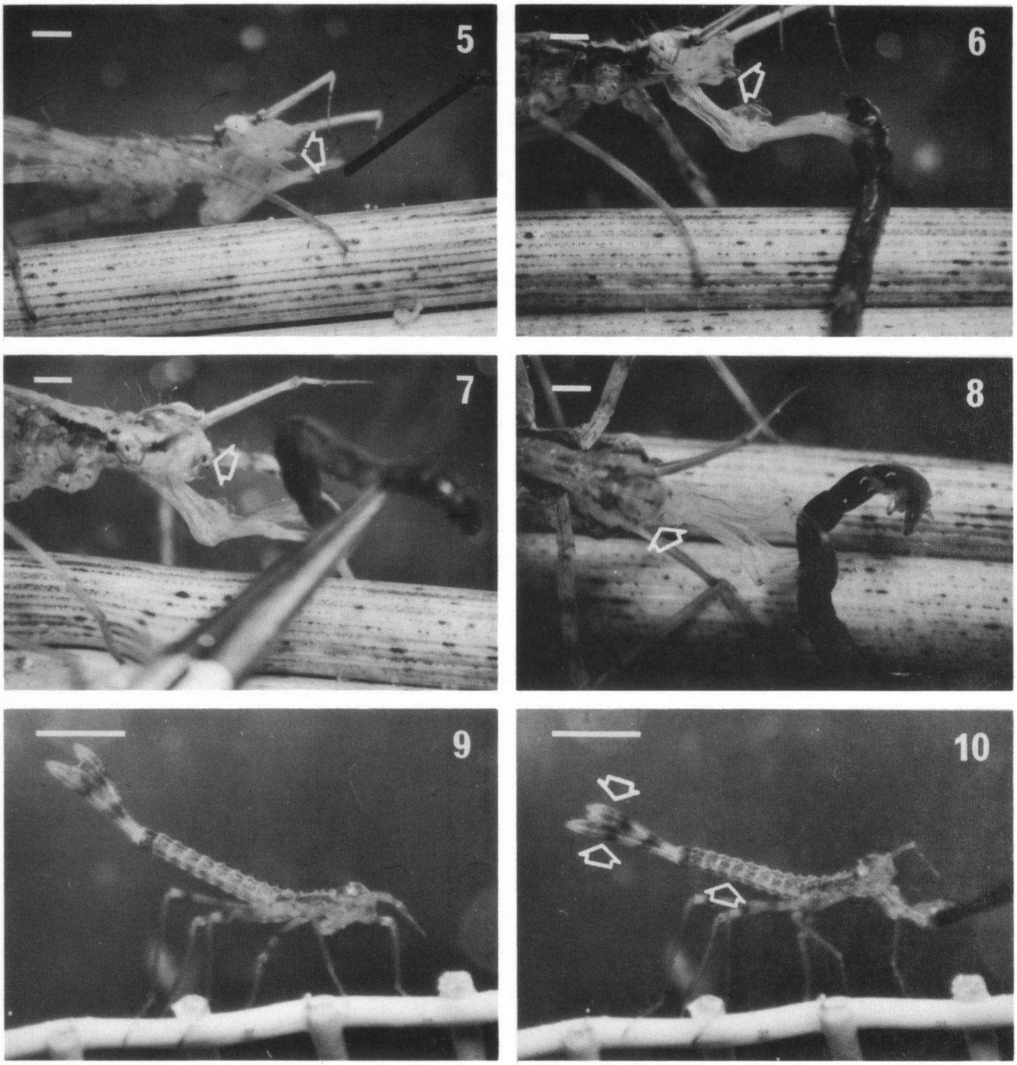


Fig. 4. In order, from top to bottom: variations of the angle between the two palps, displacement of the mentum, displacement of the digestive tract, variations in length of the abdomen, variations of the angle between the lateral caudal gills, variations of the angle between the two scapes. Along the abscissa is given the number of frames (N) before (negative numbers) and after (positive numbers) the projection of the mask. (a, b, c, ... , l, cf. text).

it seems to me, the adjustment of the capture is effected only by means of mechanical stimulation of the antennae.



Figs. 5-10. Scale: 1 mm. (5) The mask is loosened (cf. text). Note the opening of maxillae and mandibles (arrow) (cf. also figs. 6, 7, 8) and the antennae which are strongly bent (11th instar); – (6) The mask is projected towards the prey, which is grasped by the palps (11th instar); – (7-8) Full extension of the mask. The antennae are being raised (11th instar); – (9-10) Fourth instar larva before (fig. 9), and during the projection of the mask (fig. 10). Note the convergence of the gills and the contraction of the abdomen (arrows).

During capture in Aeshnid larvae (PRITCHARD, 1965), the convergent motion of epiproct and paraprocts indicates that the anal sphincter is closed. Simultaneously, a strong dorso-ventral contraction of the abdomen elicits the projection of the mask. When the prey, being grasped, has been brought to the mouthparts for ingestion, the epiproct and paraprocts open again. The same phenomenon was observed in *Agrion splendens* larvae (Figs. 9, 10). In the latter, at least, only the gizzard, the crop and the oesophagus do the piston movement, the midgut being apparently not moved during the strike . One can assume a hydraulic mechanism is involved. The contraction of abdominal muscles elicits both the raising up of the sterna and the shortening in length of the abdomen. Consequently, a sudden increase in pressure is transmitted to the haemolymph in the head, the mask being projected forward. The walls of the oesophagus and the crop being thin, an active forward contraction of these organs seems to be excluded. It seems rather that, due to their elasticity, their motion is passive caused by the overpressure.

In anisopteran larvae, where the abdomen is large, the presence of diaphragmatic muscles makes possible the canalization of the pressure. In *Agrion splendens* larvae no diaphragms exist. Thus, to the hypothesis of WHEDON (1918) who said: "the tubular arrangement and longitudinal direction of the muscles in the zygopterous larva were perfected for locomotion by wriggling from side to side", must be added that the tubular arrangement and the narrowness of the abdomen compensates for the absence of diaphragms, permitting the establishment of a hydraulic mechanism for the projection of the mask.

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